

Availability of phosphate and potassium as the result of interactions between root and soil in the rhizosphere

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Summary – Zusammenfassung

A number of findings are summarized in order to show the significance of individual plant properties and soil factors on the availability of phosphate and potassium to plants growing in soil.

The flux of a nutrient into a given plant root depends directly on the concentration of the nutrient in the adjacent solution. In nutrient solution, P and K influx follows Michaelis-Menten kinetics. Almost maximum rates of influx have been observed in the range of soil solution concentrations usually found in German arable soils. Roots exhaust P and K from solutions to about $0.2 \mu\text{mol P}$ and $1 \mu\text{mol K l}^{-1}$ if not replenished.

At the root surface P and K concentrations in soil decrease rapidly within one day; small changes occur after this period. Initially, the extent of the depletion zone is very small but it extends radially with time. After the initial phase therefore, P and K supply to the plant depends on transport from more remote parts of the soil and also on release from undissolved sources.

The degree of depletion and the extent of the depletion zone are related to the diffusion coefficient; they decrease with increasing clay content of soil. Root hairs penetrate the soil and extend the volume of soil supplying nutrients to a unit of root. P and K influx therefore increase with the length of root hairs.

Proton release of roots mobilize P and K in soil. This is clearly detected by the HCl-soluble P and K fractions within 2 mm of the root surface.

The activity of acid and alkaline phosphatases strongly increase in the soil in the vicinity of the root surface of several plant species. It is supposed that organic P compounds can therefore be utilized by plants.

P and K influx per unit of root length and root length per unit of shoot weight differed widely between species. The product of these two parameters however was closely related to the P and K concentration of the shoots.

Calculations from a mathematical model were in good agreement with measured K depletion profiles and K uptake by plants. It is therefore concluded that the main factors influencing the P and K availability of plants growing in soil have been accounted for in the mathematical model and that the parameters have been accurately measured.

Pflanzenverfügbarkeit von Phosphat und Kalium als Ergebnis von Wechselwirkungen zwischen Wurzeln und Boden in der Rhizosphäre

Es werden eine Reihe von Ergebnissen herangezogen, um die Bedeutung einzelner Pflanzeigenschaften und Bodenfaktoren für die Pflanzenverfügbarkeit von Phosphat und Kalium darzustellen.

Der Flux eines Nährstoffs in die Wurzel hängt von der Konzentration der umgebenden Lösung ab. In Nährlösungen folgt die P- und K-Aufnahme der Michaelis-Menten-Kinetik. Die P- und K-Konzentration der Bodenlösung deutscher Ackerböden führt häufig zu annähernd maximalen Aufnahmeraten. Die Wurzeln erschöpfen die Lösungen auf etwa $0,2 \mu\text{mol P}$ und $1 \mu\text{mol K l}^{-1}$, wenn sie nicht ergänzt werden.

In der Wurzelumgebung wird der Boden ebenfalls weitgehend entleert. Die räumliche Ausdehnung der Verarmungszone beträgt jedoch nur wenige mm. Innerhalb eines Tages sinkt die Konzentration rasch ab; danach ändert sie sich nur noch wenig, die Verarmungszone dehnt sich jedoch in radialer Richtung aus. Die Versorgung der Wurzeln hängt demnach vom Transport aus entfernteren Teilen des Bodens sowie von der Freisetzung aus ungelösten Vorräten ab. Der Grad der Verarmung und die Ausdehnung der Verarmungszone nimmt mit dem Tongehalt des Bodens ab.

Wurzelhaare durchdringen den wurzelnahen Boden und vergrößern den Einzugsbereich der Einzelwurzeln. Der P- und K-Influx verschiedener Pflanzenarten steigt daher pro Einheit Wurzel mit der Länge der Wurzelhaare an.

Protonen-Abgabe der Wurzeln führte zur Mobilisierung der P- und K-Vorräte. Dies ist an der Änderung der HCl-löslichen Fraktion des Bodens bis zu 2 mm Entfernung von der Wurzel deutlich nachzuweisen.

Die Aktivität der sauren und alkalischen Phosphatase weist im wurzelnahen Boden verschiedener Pflanzenarten eine starke Erhöhung auf. Es wird angenommen, daß die Pflanzen dadurch auch organische P-Verbindungen ausnutzen können.

Pflanzenarten unterscheiden sich erheblich im P- und K-Influx je Einheit Wurzellänge und in der Wurzellänge je Gewichtseinheit Sproß. Das Produkt dieser beiden Eigenschaften korreliert jedoch sehr eng mit dem P- und K-Gehalt des Sprosses; ihr Anteil an der P- und K-Versorgung ist demnach sehr unterschiedlich.

Modellrechnungen haben gezeigt, daß sowohl die K-Verarmungsprofile im wurzelnahen Boden als auch die von den Pflanzen aufgenommenen Kaliummengen mit den durch Messung erhaltenen Werten gut übereinstimmen. Demnach sind von den Faktoren, die die Pflanzenverfügbarkeit von P und K bestimmen, die wichtigeren berücksichtigt und ihre Parameter zutreffend gemessen worden.

Introduction

The supply of mineral nutrients to a crop depends on the 'availability' of nutrients in the rooting medium. The term availability has often been equated with fractions of the soil nutrients of a given solubility. As early as 1934 however, *Spencer* and *Stewart* realized that availability depends on both the chemical nature of a nutrient and its location in the soil relative to plant roots. It is therefore necessary to distinguish between chemically available and positionally available nutrients. These subterms in turn are related to the mobility of the element under investigation as can be concluded from considerations of *Bray* (1954) and *Barley* (1970). It was *Barber* (1962), who introduced the concept of mobility in relation to mass flow and diffusion. This was the basis for understanding the mechanisms involved in the movement of nutrients from the soil to plant roots and for the quantitative treatment of nutrient availability. This concept implies the ability of plants to create gradients of nutrient concentration and

water potentials in the soil surrounding roots. The living plant is therefore the driving force governing nutrient mobility in the rhizosphere. Plant properties such as water consumption and root morphological and physiological factors have thus to be regarded as being as important as chemical and physical factors of the soil for nutrient availability.

This basic concept has had a considerable impact on research within the last two decades. Numerous studies have shown that nutrient supply to a plant depends not only on the concentration of an element in soil solution and its interaction with the solid phase but also on growth, distribution and shape of the roots, as well as on their physiological ability to mobilize and absorb nutrients. Milestones in the progress of knowledge are represented by the books of *Nye and Tinker (1977)* and *Barber (1984)*.

It may now be supposed that the major factors affecting nutrient availability and their mode of action are established. The complex interaction of these factors however, has as yet prevented quantitative determination of available nutrients on a wide scale. Chemical soil testing usually takes only one factor of availability into account, that of the concentration of an element. The result is not satisfactory, except in cases of highly mobile nutrients such as nitrate, because the high mobility overrides other factors. Determination of availability on a more complex and causal basis is now being pursued by means of mathematical models (*Nye et al. 1975; Claassen and Barber, 1976; Cushman, 1979*). These models attempt to integrate all factors into a comprehensive concept. They thus enable us to verify or falsify our perception of the system as well as to evaluate the significance of the factors involved. Such models are nowadays instruments of research; their application for practical purposes is certainly a logical aim. This aim, however, can only be achieved if the factors involved and their interactions are established quantitatively.

In recent years we have studied a number of these factors influencing availability. The object of this paper is to summarize the results in order to evaluate the significance of the individual factors in understanding the availability of phosphate and potassium to plants growing in soil.

Material and Methods

The results are based on a combination of the following measurements and procedures:

- Characteristics of nutrient uptake kinetics of plant roots determined by the method of *Claassen and Barber (1974)* in solution culture which avoids interferences by the soil.
- Soil properties determining the mobility of nutrients: P and K concentration of the soil solution measured by the displacement technique of *Adams (1974)*; exchangeable and nonexchangeable K by NH_4^- and HCl-extraction; diffusion coefficients determined according to *Vaidyanathan and Nye (1966)*.
- Plant growth, nutrient uptake of the plants by pot experiments with different soils in a growth chamber; root length (*Newman, 1966*) and root hair length (*Föhse, 1985*).

- Concentration gradients around individual roots of Rb-86, isotopically exchangeable P and K by using P-33 and K-43 respectively, and quantitative autoradiography in combination with desorption studies (Claassen et al., 1981 a).
- Gradients in the soil adjoining root systems: Exchangeable K, soluble P, pH, and phosphatase activity in the rhizosphere were determined with usual methods. However, the methods were applied to soil samples of a defined distance from the root which were obtained with the thin slicing procedure of Kuchenbuch and Jungk (1982).
- Calculations by the mathematical model of Claassen and Barber (1976) by using the above mentioned independently measured soil and plant parameters in order to simulate both the depletion pattern of the soil around roots and the uptake of nutrients by the plants (Claassen et al. 1986).

Results and Discussion

P and K flux into roots as related to P and K concentration in solution

Plant roots are generally assumed to absorb mineral nutrients from soil solution. Influx therefore directly depends on the concentration (C) of a nutrient in the soil solution at the root surface. Phosphate and potassium influx is related to concentration in the form of a saturation curve which can be described by the Michaelis-Menten equation as modified by Nielsen (1976):

$$I_n = \frac{I_{\max} (C - C_{\min})}{K_m + C - C_{\min}} \quad (1)$$

I_n is the net influx of a nutrient. I_{\max} , the maximum influx, is the parameter for the capacity of a root to absorb a nutrient. K_m , the Michaelis constant, describes the affinity

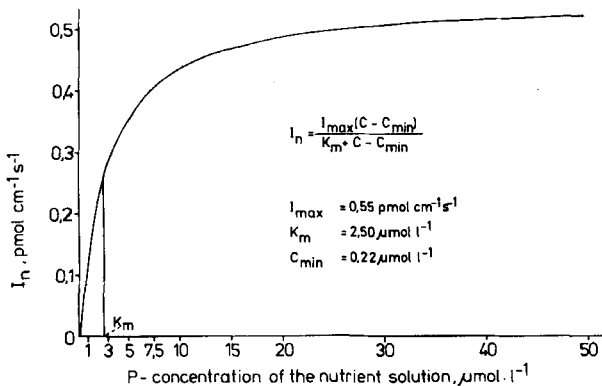


Figure 1: Phosphate influx per cm root of 28 days old maize plants in relation to the phosphate concentration of a nutrient solution (Jungk and Barber, 1975)

Abbildung 1: Phosphatinflux pro cm Wurzel von 28 Tage alten Maispflanzen in Beziehung zur Phosphatkonzentration einer Nährlösung.

of the uptake system for a nutrient. C_{\min} is the minimum concentration to which plants can deplete a solution.

An example for P uptake by 28 days old maize plants grown in nutrient solution is given in Fig. 1. The curve is calculated from data of *Jungk* and *Barber* (1975) by using equation (1). As can be seen, influx of P strongly increased with P concentration in the low range. Even at $10 \mu\text{mol l}^{-1}$ about 80 % of the maximum was achieved. On the other hand the roots are able to deplete phosphate to a level as low as $0.2 \mu\text{mol l}^{-1}$. The rate of potassium uptake in relation to K concentration followed the same type of curve, but the parameters I_{\max} and K_m were about ten times higher than for P (*Claassen* and *Barber*, 1977). C_{\min} values for K have been found between 1 and $2 \mu\text{mol l}^{-1}$. This demonstrates the high efficiency of maize roots for uptake under favourable conditions, an observation also made in other species.

Soil solutions in German arable soils are usually found in the range of 10 to $100 \mu\text{mol P}$ and 200 to $1000 \mu\text{mol K}$ per litre. It can thus be concluded that young roots growing into such soil will start to absorb P and K at a rate close to I_{\max} and the P and K in the soil solution in contact with the roots can be almost entirely exhausted of these nutrients.

The parameters governing P and K uptake kinetics are not constant. They vary depending on plant species (*Loneregan* and *Asher*, 1967; *Jungk*, 1974; *Föhse*, 1985) genotype (*Schenk* and *Barber*, 1979), plant age (*Jungk* and *Barber*, 1975) and soil temperature (*Mackay* and *Barber*, 1984). Of major influence may also be the nutritional status of the plant (*Claassen* and *Barber*, 1977; *Jungk*, 1974; *Drew et al.* 1984). As can be seen from Table 1 (*Jungk*, 1974), % P in the plant decreased as the number of days

Table 1: Effect of P starvation on P uptake parameters and total P content of 58 days old tomato plants (*Jungk*, 1974)

Tabelle 1: Wirkung von P-Mangel auf Parameter der P-Aufnahme und den Gesamt-P-Gehalt von 58 Tage alten Tomatenpflanzen

no-P treatment days	I_{\max} <u>p moles</u> cm s	K_m $\mu\text{mol l}^{-1}$	C_{\min} $\mu\text{mol l}^{-1}$	total P % in dry matter	
				shoot	root
1	0.088	4.51	0.27	1.08	0.78
4	0.109	1.06	0.20	0.89	0.63
5	0.147	1.36	0.22	0.78	0.62

increased following the withdrawal of P supply. The reaction of the plant to P starvation is to increase I_{\max} and to decrease K_m . This response leads one to the conclusion that plants adapt to low nutrient supply by increasing the efficiency of their uptake systems at low concentration.

Depletion of the soil around individual roots

The uptake of nutrients by the root creates concentration gradients in the soil perpendicular to the root axis. In order to obtain information on shape, size and development of these gradients, ion distribution around individual roots were measured by quantitative autoradiography using ^{33}P and, as a tracer for potassium, ^{86}Rb . As can be seen from Fig. 2, isotopically exchangeable phosphate was reduced to 50 % of the

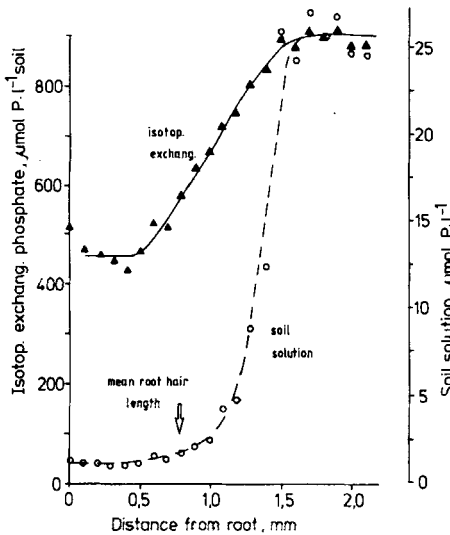


Figure 2: Concentration of isotopically exchangeable phosphate and phosphate concentration of the soil solution in the vicinity of a maize root 3 days old (Osterwald sandy soil) (Hendriks et al., 1981)

Abbildung 2: Isotopisch austauschbares Phosphat und Phosphatkonzentration der Bodenlösung in der Umgebung eines 3 Tage alten Maiswurzelschnittes (Sandboden Osterwald)

initial concentration at the surface of a maize root section within 3 days. This depletion amounts to 420 kg P ha^{-1} if a soil layer of 30 cm were exhausted to the same extent. However, the depletion zone extends to a distance of 1.5 mm only. Assuming a root density of 3 cm cm^{-3} it can be calculated that about 20 % of the top soil volume contributes P to the crop in one season. This fraction of the 420 kg P ha^{-1} is therefore positionally available.

By using the desorption isotherm the P concentration of the soil solution was also determined. This value (Fig. 2) was reduced from 26 to $1 \mu\text{mol P l}^{-1}$ at the root surface. The lower value is somewhat but not much higher than C_{min} found in solution culture (Fig. 1). This indicates that P transport from the soil to the root was not sufficient to replenish soil solution P at the root surface while roots were absorbing P.

Similar profiles were found for the Rb depletion by maize roots as shown in Fig. 3. However, the depletion zone of Rb extended to a considerable greater distance from the root than of phosphate after similar periods of time. The mobility of Rb (K) is therefore higher than for P. This is in agreement with the diffusion coefficients being in the order of $10^{-7} \text{ cm}^2 \text{ s}^{-1}$ for K (Rb) and $10^{-9} \text{ cm}^2 \text{ s}^{-1}$ for phosphate ions in soil.

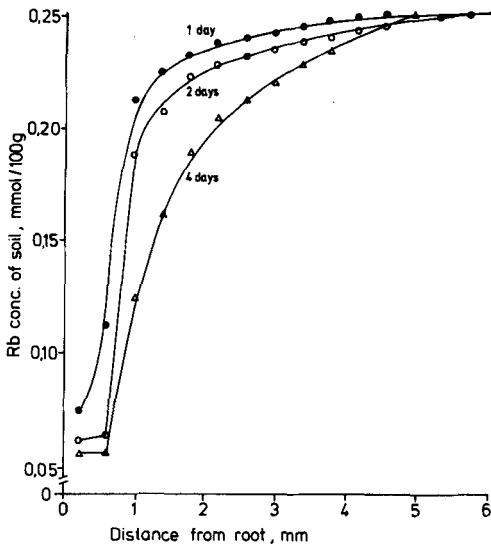


Figure 3: Rb depletion of a sandy soil by maize at different age of a root section (Herrenhausen sandy soil) (Claassen et al., 1981 b)

Abbildung 3: Rb-Verarmung eines Sandbodens durch Mais bei unterschiedlichem Alter eines Wurzelabschnitts (Sandboden Herrenhausen)

As also shown in Fig. 3, the Rb concentration of the soil at the root surface decreased markedly within one day; only small changes occurred after this period. Initially the width of the depletion zone was very small. It extended in the following days in a radial direction.

This type of result was also obtained for P (Hendriks et al., 1981). It must therefore be concluded that after the initial phase P and K flux into the plant is limited by transport from more remote parts of the soil rather than by the uptake parameters of the root. The amount of P and K available to a unit of root depends on both the decrease of concentration at the root surface and the width of the depletion zone. Both of these aspects may be influenced by soil and plant properties.

Soil properties affecting depletion around roots

a) Soil texture

The availability of potassium is known to depend on soil texture. The influence of this factor on the Rb depletion profile has been studied with the same autoradiographic technique by using 3 soils of different clay content after application of 0.5 mmol Rb/100 g soil (Claassen et al., 1981 b). As can be seen from Fig. 4, clay content had a strong influence on soil depletion. At the root surface 66 % of the applied Rb was released by the sandy soil but only 20 % from the silt loam. In addition, the maximum extent of the depletion zone was 2 mm in the heavy but about 4 mm in the light textured soil.

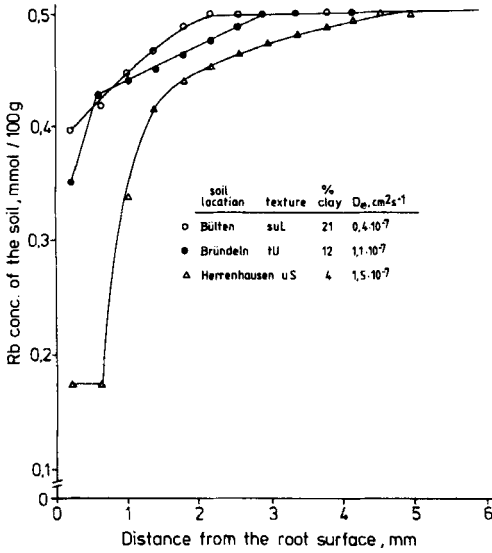


Figure 4: Rb depletion profiles around maize root sections 3 days old in soils of different texture (Claassen et al., 1981 b).

Abbildung 4: Rb-Verarmung von Böden unterschiedlicher Textur durch Maiswurzelabschnitte nach 3 Tagen

Equation (2) approximates the relation between the diffusion coefficient and distance of diffusion

$$\Delta X = \sqrt{2 D_e t} \tag{2}$$

where

ΔX = distance of diffusion, cm

D_e = effective diffusion coefficient, $\text{cm}^2 \cdot \text{s}^{-1}$

t = time, s

The result in Fig. 4 is in fairly good agreement with equation (2) if the width of the depletion zone is taken in the range of 0–20 % of maximum depletion.

b) Buffer power

Solute movement from the soil to the plant root proceeds by mass flow and diffusion. Because P and K concentration in the soil solution is low compared to the plant, mass flow can be neglected here. The mobility of ions moving by diffusion is determined by the effective diffusion coefficient D_e which is defined by Nye and Tinker (1977):

$$D_e = D_1 \cdot \Theta \cdot f \cdot \frac{dC_1}{dC} \tag{3}$$

where

D_1 = the diffusion coefficient in water

Θ = volumetric water content

f = impedance factor

C_1 = concentration of the nutrient in solution

C = quantity of the nutrient participating in diffusion
 dC/dC is the reciprocal of the buffer capacity

In Order to determine the relation of C to C_1 , desorption curves were established for the three soils used in Fig. 4. As shown in Fig. 5, the Rb concentration of the equilibrium solution was much higher in the sandy than in the heavier soils. Even under the soil depletion at the root surface shown in Fig. 4, which is total Rb in the soil, Rb concentrations in solution remained higher in the sandy than in the two other soils. The values at the root surface were 15, 5 and 3 $\mu\text{mol Rb l}^{-1}$ soil solution respectively, as can be determined by comparing Fig. 4 and 5. The root could therefore sustain a higher influx per unit of root length in the sandy soil.

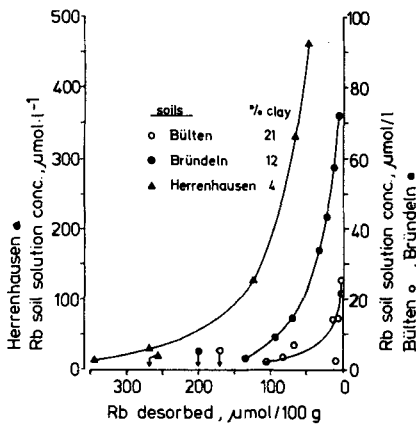


Figure 5: Rb desorption curves of three soils of different texture after application of 500 $\mu\text{mol Rb}/100\text{ g}$ soil. Arrows indicate NH_4 -exchangeable Rb (Claassen et al., 1981 b)

Abbildung 5: Rb-Desorptionskurven von Böden unterschiedlicher Textur nach Zugabe von 500 $\mu\text{mol Rb}/100\text{ g}$ Boden. Pfeile bezeichnen das durch NH_4 austauschbare Rb

On the other hand, as also seen in Fig. 5, the sandy soil released a much higher percentage of the applied Rb into solution when the equilibrium concentration was reduced to the same level as the two other soils. The effect of soil texture on both soil depletion and influx of K/Rb can thus be quantified by knowing buffer curves and soil depletion profiles.

c) Nonexchangeable potassium

It has long been recognized (Schachtschabel, 1937) that the (by NH_4^+) nonexchangeable potassium may play a part in the potassium nutrition of plants. However, the influence of plant roots on the mobilization and the conditions necessary for the release of this fraction is not well understood.

In order to study this process in the soil-root interface a method was used by which soil samples may be obtained from defined distances from the root surface (Kuchenbuch and Jungk, 1982). As can be seen from Fig. 6 (Kuchenbuch and Jungk, 1984), rape seedlings depleted HCl soluble K to a much higher degree than the NH_4 -exchangeable

K fraction but only within a distance of 2 mm from the root surface. The plants therefore extracted a considerable amount of K from the 'nonexchangeable' K of the soil within the first 7 days of growth. If one assumes a root density of 4 cm^3 and the depletion profile of Fig. 6 is directly applied to individual roots, about 50 % of the total soil volume contributes K to the plants from this fraction.

Desorption studies of Claassen and Jungk (1982) with the same soil showed a strong release of nonexchangeable K after the K concentration of the solution in contact with the soil had been reduced to $2\text{--}3 \mu\text{mol l}^{-1}$. The ability of plant roots to deplete their surroundings to very low concentrations therefore appears to be essential for the release of nonexchangeable K.

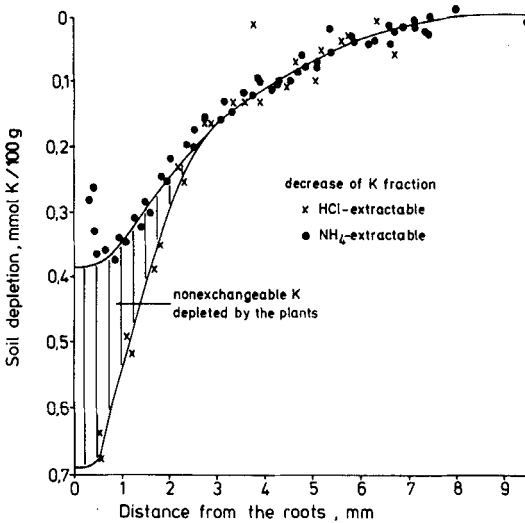


Figure 6: Depletion profiles of NH_4^- and HCl-extractable soil potassium in the rhizosphere of rape seedlings 7 days old (Söderhof silt loam) (Kuchenbuch and Jungk, 1984)

Abbildung 6: Verarmungsprofile der NH_4^- und HCl-extrahierbaren K-Fraktion eines Lehmbodens durch 5 Tage alte Rapswurzeln (Boden Söderhof)

Plant properties affecting soil depletion around roots

a) Root hairs

The shape of the curves in Fig. 2 and 3 cannot be explained solely by diffusion from the soil to the root cylinders because if this were the case then the slope should be steepest at the root surface. The extent of the almost uniformly depleted zone in Fig. 2 is about equal to the length of root hairs (see arrow in Fig. 2). Using different plant species Rb depletion profiles were found to extend to distances related to the root hair

length (Claassen and Jungk, 1984). It may therefore be supposed that the volume of soil which can be depleted by a unit of root length is influenced by root hair length. If this is important for the nutrition of plants the rate of uptake of a root section should also be influenced.

In studying this question Föhse (1985) found indeed a significant influence of root hair length on the rate of P influx expressed as a percentage of maximum influx (Fig. 7). In a P deficient soil plants with long root hairs can therefore satisfy a higher percentage of their P demand than plants with short root hairs, provided that root length per unit of shoot weight is the same.

Relationships between P uptake and root hair formation were also found in several but not in all cases by Schenk and Barber (1979) and Itoh and Barber (1983). A lack of a close correlation may be explained by equation (2). This equation leads to the prediction that root hairs should be important only if D_e is small and thus the distance of diffusion in a limited period of time is small. This is generally the case under low P supply where D_e is in the order of 10^{-9} cm^2s^{-1} . For the same reason root hairs are expected to be less important for the K than for the P supply of plants. As shown in Fig. 3 and 4 and as can be calculated from equation (2), potassium diffuses in 3 days over distances of several mm under moist conditions. The mobility of K in many soils should thus override the effect of root hairs.

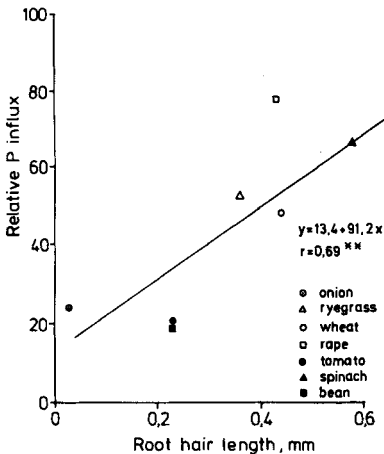


Figure 7: Influence of root hair length on P influx of different plant species per unit of root length in percent of maximum influx. Holtensen loess subsoil supplied with 5 mg P/100 g soil for relative P influx, 40 mg P/100 g soil for maximum P influx (Föhse, 1985)

Abbildung 7: Einfluß der Wurzelhaarlänge auf den P-Influx verschiedener Pflanzenarten pro Einheit Wurzellänge in % des maximalen P-Influsses. P-armer Loess-Unterboden (Holtensen) bei einer P-Düngung pro 100 g Boden von 5 mg = relativer P-Influx, 40 mg = maximaler P-Influx

b) Root induced pH changes in the rhizosphere

Net proton extrusion of roots is regarded to be another strategy by which plants acquire nutrients of low solubility (Nye and Tinker, 1977). We started to study P depletion by the technique of thin slicing soil. Rye grass seedlings were supplied with different nitrogen sources in order to influence net proton release of the plants. Some of the results (Singh, unpublished) are summarized in Fig. 8. The decrease of pH as the

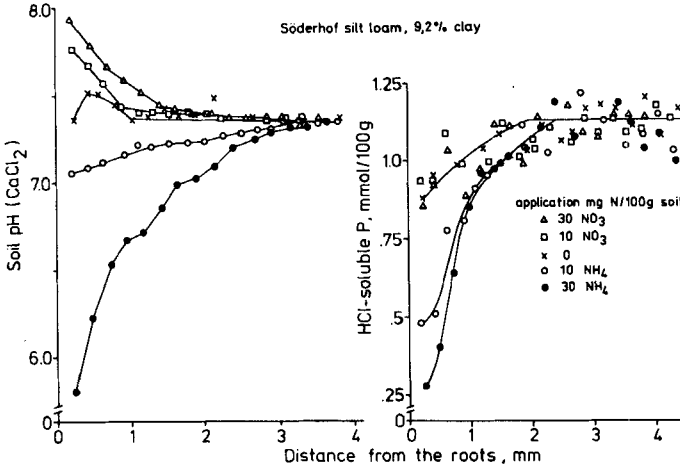


Figure 8: pH change and P depletion in the rhizosphere of ryegrass as influenced by ammonium and nitrate nitrogen (Singh, unpubl.)

Abbildung 8: pH-Veränderung und P-Verarmung in der Rhizosphäre von Weidelgras unter dem Einfluß von Ammonium- und Nitrat-Stickstoff

result of $\text{NH}_4\text{-N}$ nutrition was obviously related to the marked increase of depth and width of the P depletion zone. The quantity of phosphate available per unit of root can thus be considerably increased. This is in agreement with calculations of Nye (1984).

The release of nonexchangeable K as in Fig. 6 may also be influenced by the presence of protons which may replace K in interlayer positions. This view is supported by the result of Kuchenbuch (1983, p. 75) that the soil region which released nonexchangeable K was markedly acidified. The rise of pH in the rhizosphere which, with nitrate nitrogen nutrition, is brought about by net HCO_3^- release by the roots, may also increase the availability of P as has been found by Föhse (1985) and Wydra (unpublished).

The ability of plants to change the pH in the soil-root interface therefore appears to be important in influencing the availability of P and K as has also been observed in Fe and Mn by Marschner et al. (1986).

c) Phosphatase

Even though as much as one half of total P in soil may consist of organic compounds, the role of this fraction in soil as a P source of plants is still uncertain. Recent data of Helal and Sauerbeck (1984) suggest a considerable turnover of inorganic into organic P in the rhizosphere. On the other hand, enzymes which can hydrolyze such compounds have been detected in soil many years ago. Not much, however, is known of the reactions of organic P in the rhizosphere.

In order to study this problem the activity of phosphatases in the soil around plant roots was measured (Tarafdar and Jungk, 1986). As shown in Fig. 9, acid phosphatase activity at the root surface is much higher than in the bulk soil for some plant species. Similar results were found for the alkaline phosphatase, which is produced by microorganisms only. Additional experiments of Tarafdar and Claassen (1986) have shown, that a number of organic phosphate compounds are readily hydrolyzed in the growth medium. They also proved to serve as P sources for plants.

These results suggest that plants are able to hydrolyze organic phosphates by means of phosphatases in the rhizosphere. Organic P may therefore be more important in the P nutrition of plants than has previously been thought.

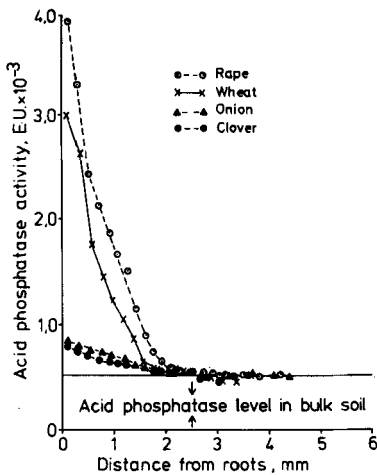


Figure 9: Distribution of acid phosphatase activity in the rhizosphere of different plant species (Börry silt loam) (Tarafdar and Jungk, 1986)

Abbildung 9: Verteilung der Aktivität der sauren Phosphatase in der Rhizosphäre verschiedener Pflanzenarten (Boden Börry, schluffiger Lehm)

Nutrient uptake of whole plants

The properties of plants mentioned above result in a given influx per unit of root and a given quantity of nutrients taken up in the period a root section is active. If the depletion zone around a root is small and the distance between roots is large then only part of the rooted soil layer will provide P and K for the crop. The supply to the shoot will then be influenced by the amount of roots feeding the shoot i.e. root/shoot ratio. The period of time roots take up nutrients may also be of influence as has been shown by Claassen and Jungk (1984). Hence, if whole plants are considered, these factors have to be taken into account, especially the root/shoot ratio.

Using a P deficient loess soil (see Fig. 7) and suboptimal P application, Föhse (1985) found large differences between 7 species for both influx of P per unit root length and length of root per unit of shoot (Fig. 10). Neither root length nor influx alone was closely related to the P concentration of the shoot; their product, however, gave a

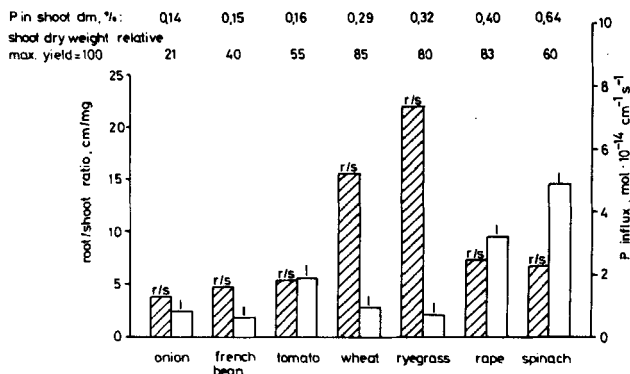


Figure 10: Root/shoot ratio (*r/s*) and P influx (*I*) of different plant species. Relative shoot weight was obtained with 5 mg P, maximum shoot weight 40 mg P per 100 g of Holtensen loess subsoil (Föhse, 1985)

Abbildung 10: Wurzel/Sproß-Verhältnis (*r/s*) und P-influx (*I*) verschiedener Pflanzenarten. Relative Trockenmassebildung wurde erzielt durch 5 mg P, die maximale T.M.-Bildung durch 40 mg P-Düngung pro 100 g des P-armen Loess-Unterbodens Holtensen

correlation coefficient of as high as $r = 0.97$. Similar results were obtained for potassium (Claassen and Jungk, 1984). Hence, of the plant factors, these two seem to be most important for the supply of P and K to the shoots.

The two gramineae (Fig. 10) exceed all other species in root length per unit shoot but their P influx is low. Such a root system appears to be efficient in a soil of low P mobility. The high root density ensures that a high percentage of the soil P is positionally available. The low influx results in a low rate of depletion of the soil at the root surface and thus maintain a high percentage of the maximum influx over relatively long periods. In contrast, rape and spinach having higher influx and less roots, depend more on the P uptake efficiency per unit of root rather than on root length. Onion, french bean and tomato have low values for both parameters and can thus be regarded as inefficient root systems. These plants need high phosphate mobility in soil. This is evident from the small relative shoot weight they attained with 5 mg P application per 100 g soil compared to the maximum shoot weight found with 40 mg P application per 100 g soil.

Calculation of availability by mathematical models

If the processes involved and the factors affecting nutrient availability are quantitatively known it should be possible to simulate uptake mathematically. Based on an equation of Nye and Marriott (1969), Claassen and Barber (1976) developed a model to calculate nutrient uptake of plants from the soil. It is based on mass flow and diffusion as the mechanisms of ion transport from the soil to plant roots and on Michaelis-Menten

kinetics of nutrient absorption by plant roots. Ten parameters of soils and plant properties were used. In addition, *Cushman* (1979) included root density as another parameter to account for interroot competition resulting from the overlap of depletion zones. The parameters needed are: for the soil, C_{ii} soil solution concentration, D_e and b and for the plant, I_{max} , K_m , C_{min} , r_o root radius, r_1 distance between roots, v_o water influx, k the root growth constant and L_o initial root length.

In order to verify the model *Claassen et al.* (1986) have applied it to describe potassium depletion by rape roots of a silt loam soil with 3 K levels. The data were measured by the thin slicing technique with subsequent extraction with NH_4OAc to determine exchangeable K (*Kuchenbuch and Jungk*, 1984). As can be seen from Fig. 11, there is a good agreement between the measured data and the calculated curves. It should be emphasized that the curves are the result of calculations of this mechanistic model and are not simply a statistical fit of the data.

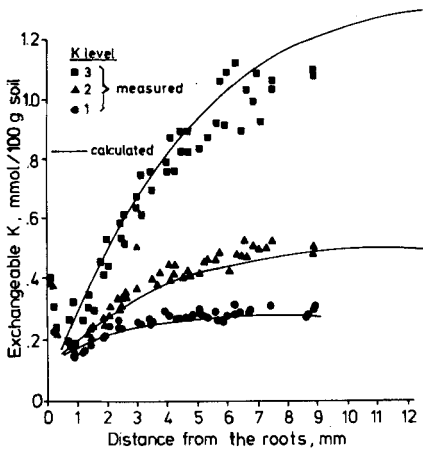


Figure 11: Measured and calculated K depletion of the soil in the vicinity of rape roots 4 days old at three different K levels (Söderhof silt loam) (*Claassen et al.*, 1986)

Abbildung 11: Gemessene und durch Modellrechnung gefundene K-Verarmungsprofile in der Umgebung 4 Tage alter Rapswurzeln bei 3 K-Stufen im Boden Söderhof (schluffiger Lehm)

The model was also used to predict K uptake of maize plants grown in a pot experiment with the three different soils used for the experiments described in Fig. 4 and 5, each soil with two different K levels. As can be judged from Fig. 12, this calculation also agreed satisfactorily with the quantity of K in the shoot measured by plant analysis.

It can therefore be concluded that the major factors affecting K uptake of plants are taken into account by the model and the parameters have accurately been measured. The model can thus also be regarded suitable to describe processes and interactions in the rhizosphere which cannot be measured. *Kuchenbuch et al.* (1986) have applied the model to investigate how soil water content influences the behaviour of potassium in the rhizosphere. Using a silt loam soil the calculation has shown that water content strongly influences the gradient of potassium concentration at the root surface. If the soil is dry, a rapid depletion at the root surface is predicted because of the restricted K diffusion

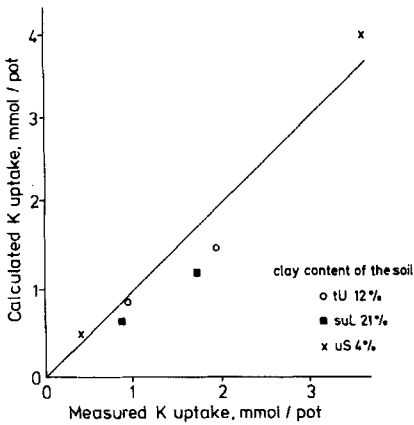


Figure 12: Measured and calculated K uptake of maize plants in a pot experiment with three soils and two K levels (Claassen et al., 1986)

Abbildung 12: Gemessene und berechnete K-Aufnahme von Maispflanzen in einem Gefäßversuch mit 3 Böden und je zwei K-Stufen

from remote parts of the soil. As a result influx is soon reduced. In contrast, a water content in the range of field capacity enables K diffusion to largely replenish the K absorbed by the roots. K concentration at the root surface is therefore kept at levels sufficient for almost maximum influx.

Model calculation therefore appears to be a useful tool for understanding and quantifying the processes and interactions in the soil-root system involved in the complex phenomenon of the availability of P and K in soil.

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